posterior to the mid-length of the bone. Anterolaterally the parietal sutures with the postfrontal in a posterolaterally slanted suture. Posterolaterally, the suture with the supratemporal is more or less parallel to the midline on the right side of the skull and posteromedially slanted on the left side of the skull. The posterior border of the parietal is also different on either side of the midline. On the right it is almost straight and transverse while on the left medially it projects into the postparietal and lateral to this rounded projection it is almost straight and transverse, so that the posterior limit of the parietal forms a rough point.

The supratemporal: The anterior limit of the supratemporal forms medially an almost straight transverse suture with the prefrontal and laterally a posterolaterally directed sinuous suture with the postorbital. Medially on the left side of the skull the supratemporal sutures with the parietal in a posteromedially directed suture. Laterally the supratemporal sutures meet with the squamosal in a sinuous suture almost parallel to the midline. The posterior limit of the supratemporal medially is a curved suture with the postparietal, while laterally the suture with the tabular is straight and then turns suddenly posteriorly so that the supratemporal forms a sharp point between the tabular and postparietal.

The squamosal: Anterolaterally the squamosal meets the jugal in a curved posterolaterally directed suture. Anteromedially the squamosal sutures with the postorbital in a sinuous anteromedially directed suture so that anteriorly the squamosal has a finger-like projection between the jugal and postorbital. Anteromedially the squamosal meets the supratemporal in a sinuous suture almost parallel to the midline. Posteromedially the squamosal meets the tabular in an almost straight suture also parallel to the midline on the right and curved on the left. The lateral limits of the squamosal are not preserved. The squamosal forms most of the dorsolateral border of the skull then turns through 90° to form a large occipital flange whose lateral edge forms the dorsolateral wall of the otic recess. In occipital view the ventral edge of the squamosal meets the occipital flange of the quadratojugal (which is not seen on the skull roof) in a straight almost transverse suture.

The postparietal: Anteriorly the postparietal sutures laterally with the supratemporal in a posterolaterally slanted suture and medially on the left side of the skull in a posteromedially slanted suture. On the right side of the skull, the postparietal seems to have pushed the parietal anteriorly so that it appears larger than the left postparietal. The medial limit of the postparietal lies on the midline of the skull. The lateral suture with the tabular is almost straight and parallel to the midline. The postparietal forms the posterior border of the skull table and then turns through 90° to form an occipital flange which ventrally sutures with the vertical flange of the exoccipital. Seen posteriorly, the ventromedial limits of the post-parietals form the roof of a transversely elongate opening that probably housed a cartilaginous supraoccipital. The ventrolateral edge of the post-parietal in occipital view forms the medial border of the posttemporal fenestra. Dorsolaterally, the postparietal sutures with the occipital flange of the tabular in a straight, dorsolaterally slanted suture.

The tabular: The tabular forms a slightly curved suture anteriorly with the supratemporal. Medially it meets the postparietal in a straight suture parallel to the midline. The lateral suture with the squamosal is also straight and parallel to the midline on the right. The tabular forms part of the posterior border of the skull table, then turns through 90° to form an occipital flange which joins with the dorsolateral flange of the exoccipital, in an interdigitated angled suture. Ventromedially, the tabular forms the lateral and dorsal borders of the posttemporal fenestra. Ventrolaterally the tabular forms the dorsolateral corner of the otic recess. Seen posteriorly, the tabular meets the squamosal in a straight dorsolaterally slanted suture.

The exoccipital: Seen posteriorly, each exoccipital forms a rounded condyle from which two thick processes rise dorsally and one thinner process laterally. The exoccipital condyles project 5cm beyond the edge of the skull table. Anterolateral to the condyle is a large foramen for the exit of the Xth nerve and just posterolateral to this is a second smaller foramen for the exit of the XIIth nerve. The ventromedial limit of the skull is formed by a flange of the exoccipital which meets between the condyles. The medial parts of this flange are not preserved. The vertical postparietal process of the exoccipital has two medial extensions, the larger dorsal one, the processus lamellosus evidently underlay a cartilaginous supra-occipital. The ventral process, the processus basalis, which is a small, sharp projection, overlies the space presumably occupied by the cartila-ginous basioccipital. Thus the true foramen magnum is smaller and narrower than the dorsal opening with its long axis transverse to the midline. The ventral border of the post-temporal fenestra is formed by the exoccipital. The dorsal suture of the exoccipital with the postparietal is sinuous and almost transverse. Dorsolaterally the exoccipital meets the tabular in a suture which has an acute angle halfway along its length. The dorsolateral limit of the exoccipital forms the ventromedial border of the otic recess. The lateral process of the exoccipital meets the pterygoid in a dorsolaterally directed suture.

In palatal view each exoccipital forms a rounded condyle posteriorly and extends anterolaterally to suture with the pterygoid in an interdigitating posterolaterally directed suture. Its medial suture with the body of the parasphenoid is curved and interdigitated.

3.2.4.2 The Sculpture

The surface sculpture is exceptionally well preserved, consisting of round or rectangular pits in the centres of ossification from which ridges and grooves radiate outward. Along some of the longer grooves cross struts have formed. A striking feature of the sculpture occurs on the postparietals and parietals where the sculpture pattern forms two triangles with their bases on the midline and the apices extending laterally towards the quadrates. The anterior angle of each triangle extends into the parietal and fades before reaching the parietal foramen. This pattern is different from that of *Hadrokkosaurus bradyi* (Welles and Estes 1969), where the sculpture pattern is also triangular and extends to the midline of the frontals. However, both patterns include the centres of the postparietals.

3.2.4.3 The Lateral Line System

The lateral line system conforms to Watson's (1956) illustration of *B. browni* except for one detail: within the left postfrontal three separate canals are visible and not two. The new canal is almost parallel to the midline, extending from just behind the anterior one-third of the postfrontal and fading just anterior to the posterior suture of that bone. It lies between the temporal and the supraorbital canal.

The Supraorbital Canal This canal forms an hour-glass pattern in the centre of the skull. Posteriorly each groove enters the anterolateral corners of the parietals. From this point the groove curves laterally passing through the postfrontal. It then swings medially into the frontal. Halfway along the length of the frontal the groove changes direction and curves laterally again to exit from the frontal at its anterolateral corner. The groove then continues laterally into the prefrontal, where anteriorly it changes direction again, curving medially to exit the prefrontal at its anterior suture. The groove continues into the nasal following the curve of the naris. It fades at the medial border of the naris.

The Temporal Canal The temporal canal issues from the postorbital and circles the orbit anteriorly giving off a posteriorly directed branch which crosses the postorbital at its posteromedial corner, and passes into the supratemporal and enters the tabular midway along the suture. The temporal canal which passes into the postfrontal sends off another branch which swings posteriorly to enter the anterolateral corner of the supratemporal where it stops. Also from the postorbital a lateral branch extends onto the jugal where it turns posteriorly and extends along the lateral part of the squamosal.

3.2.4.4 The Palate

Unless otherwise stated the left side of the skull is described. The antero-lateral borders of the palate are not preserved. Further preparation has revealed detail of the palate not previously described. A striking feature is the presence of a large foramen situated in the centre of the vomer on the midline. The position of this foramen seems to correspond to the cartilaginous area in Hadrokkosaurus bradyi (Welles and Estes 1969). In Batrachosuchus watsoni (Haughton 1925) a depression in the vomer is indicated by Watson (1956) and Welles and Estes (1969), but this depression is more posterior than the foramen found in B. browni. This foramen probably housed a gland. It is roughly triangular with the apex pointing posteriorly. The base is 9mm across and the midline length is 9mm.

The matrix has not been removed from the subtemporal vacuities, due to the delicacy of the surrounding bones and the overlying skull roof.

The vomers The most anterior limits of the vomers are not preserved. In the anterolateral corner of each vomer, a large tusk next to a tusk depression is present. Posterolateral to the tusk the suture with the palatine is interrupted by the choana. The vomer forms the anteromedial border of the choana. From the posteromedial corner of the choana the suture with the palatine slants posteromedially to the anterolateral corner of the interpterygoid vacuity. A vomerine foramen lies in the centre of the vomers as described above. The posterior ends of the vomers project on either side of the cultriform process of the parasphenoid. There is no depression in this area as in Batrachosuchus watsoni, but the two elements blend smoothly together.

The palatine The most anterior limits of the palatine are not preserved.

Anteromedially, an anterolaterally directed suture with the vomer leads off the anterolateral corner of the choana. The palatine forms the postero-lateral border of the choana. Posteromedially, the suture with the vomer extends from the posteromedial corner of the choana to the anteromedial corner of the interpterygoid vacuity. Posterolateral to the choana is a large tusk adjoining a broken tusk base. Posterolateral to the pair of tusks the sinuous anterolaterally directed suture with the ectopterygoid is visible extending to the anterolateral corner of the interpterygoid vacuity. The palatine forms most of the anterior border of the inter-pterygoid vacuity.

The ectopterygoid The anterolateral limits of the ectopterygoid are not preserved. The ectopterygoid sutures with the palatine anteromedially in a sinuous anterolaterally directed suture. Posteromedially the ectoptery-goid borders the anterolateral corner of the interpterygoid vacuity. Two teeth (tusks) smaller than the vomerine and palatine tusks are present just lateral to the anterolateral corner of the interpterygoid vacuity. Posteriorly, an interdigitated almost straight transverse suture with the pterygoid enters the anterolateral border of the interpterygoid vacuity

The parasphenoid The parasphenoid forms a large polygonal body under-lying the exoccipitals posteriorly and the pterygoids laterally. The body is smooth and slightly concave. Two grooves following the lateral margins of the cultriform process extend into the body, at the centre of which is a very shallow transverse depression which is probably homologous with the crista muscularis of the capitosaurs. The cultriform process is broad and flat. It narrows from 4.2cms at its base to 1.9cms almost halfway along its length. The process then broadens to 2.5cms at its anterolateral sutures with the vomers. Anteriorly the cultriform process forms a point in the midline from which the anterolateral sutures slant backwards in a posterolateral direction. The parasphenoid does not extend to the posterior limit of the skull as it does in Batrachosuchus watsoni, but leaves a gap of 1cm from this border. The quadrate is missing.

The Pterygoid The pterygoid displays the typical condition found in the brachyopids in that the lateral edge of the palatine flange turns through 90° forming the vertical inner wall of the subtemporal vacuity. In palatal view, the body of the pterygoid has an interdigitated slightly curved suture with the body of the parasphenoid. Posterolaterally, the pterygoid sutures with the exoccipital in an almost straight posterolaterally directed suture. The quadrate ramus of the pterygoid is expanded so that the posterolateral corner of the vertical flange lies 1.2cms posterior to the edge of the palatal portion.

In occipital view the pterygoid sutures medially with the exoccipital in a dorsolaterally slanted suture. In then extends laterally forming the ventral border of the otic recess before turning vertically. A part of the parotic plate of the pterygoid is visible on the dorsolateral surface of the pterygoid (as in Batrachosuchus watsoni, illustrated by Watson, 1956).

The Choanae The right choana measures 1.8cms at its narrowest breadth by 2.6cms at its long axis. The anterior limits of the left choana are not preserved and the shape seems to be distorted. The right choana has its long axis transverse to the midline.

The Interpterygoid vacuity The interpterygoid vacuity has its greatest width along its anterior border. The right measures 6.1cms at its anterior border by 10cms; the left measures 5.6cms at its anterior border by 10cms, this discrepancy being due to distortion.

The Subtemporal vacuity The subtemporal vacuity is obscured by matrix which if removed may endanger the skull roof. Its inner border is formed by the vertical flange of the pterygoid.

3.2.5 Discussion

When comparing B. browni to B. watsoni confusion is encountered (see Table IX) as the three existing sets of plates and illustrations of B. watsoni show different skull proportions; e.g. in Watson's (1919) plate which is "½ approximately", the skull length is 19.2cms, whereas in Watson's 1956 reconstruction the skull length is 16cms. In Welles and Estes (1969) their new reconstruction of the skull length is only 11.5cms, but this is taken from new casts provided by the British Museum of Natural History and probably provides the most reliable information. However, when comparing the plate of Watson (1919) showing B. watsoni, to B. browni which has undergone further preparation, the two skulls look very similar and the possibility exists that they are of the same species. This would explain away the inconsistency of there being two sympatric species of brachyopid in the same horizon (Cynognathus zone). Excluding the general skull morphology which is difficult to assess for reasons already given, there are supposedly four main differences; these are:

(1) the presence of an interfrontal in B. browni;

(2) the presence of a vomerine foramen in B. browni;

(3) the parasphenoid does not reach the edge of the palate as it does in B. watsoni;

(4) the wider lateral line canals of B. watsoni and their distribution.

Looking at the plate of B. watsoni, the area where an interfrontal would be found is rather unclear but it seems that there is a possibility that sutures of an interfrontal are in fact discernible. This point could be resolved with microscopic examination of the area.

Considering Watson's (1919) plate showing the palate, in the position of the vomerine foramen found in B. browni, a distinctly triangular depression is visible. Although Welles and Estes (1969) describe the area as a depression, perhaps further preparation, if possible in this area, would uncover a foramen in B. watsoni.

The parasphenoid of B. watsoni may not reach the edge of the palate. In Watson's (1919) plate there seems to be a suture running just anterior to that margin. The wider lateral line canals could be due to a lateral compression which widened the canals, or B. watsoni may be a young individual and perhaps the lateral line canals would close together as the animal got older. The variation of their distribution may also be due to sexual dimorphism or individual variation. However, there is no evidence as yet available to verify these theories and as the wider lateral line canals of B. watsoni could have been an adaptation to faster flowing water (there is geological evidence to believe this was the case) speciation may well have occurred even though the two localities are approximately 35 miles apart.

Thus, until these four characters are explained away, it seems advisable to retain the two South African species and Welles and Estes (1969) indices are used by the author for comparisons.

3.3 Summary and Conclusions

1. The family Brachyopidae, which in South Africa is part of the Cynognathus zone fauna of the Beaufort series, may be defined as: labyrinthodonts; orbits large; palate Ω-shaped; retroarticular process long; skull outline more or less parabolic; occipital condyles project far behind posterior edge of skull roof; no zones of relative intensive growth; basicranial joints absent; pterygoids joined by suture to parasphenoid; palatal teeth present on vomer and palatine.

2. Only one genus Batrachosuchus is represented in Southern Africa by three species: B. browni and B. watsoni from the Cynognathus zone of South Africa and B. concordi from the N'tawere Formation in the Upper Luangwa Valley, Zambia. The genus may be defined as brachyopids with broad

TABLE IX

DIFFERENCES IN MEASUREMENTS OF THE THREE ILLUSTRATIONS OF BATRACHOSUCHUS WATSONI

	Watson 1919 cms.	Watson 1956 cms.	Welles and Estes 1969 cms.
Interorbital breadth, A	9.8	7.2	5
Breadth of skull roof across quadratojugals, B	27.5	18.5	16.5
Midline postorbital length, D	12.2	10	7
Midline distance between nostrils and orbits, F	2.2	1.4	1
Height of parasphenoid, H	-	4.2	3.5
Internarial breadth, J	2	1.5	1.1
Length of skull roof, L	19.2	16	11.5
Midline preorbital length, O	4.4	2.7	2.4
Distance behind orbits of parietal foramen, P	6	5	3.3
Length of body of pterygoid, Q	5	3.8	3.4
Breadth across pterygoids at concavity, R	20.8	12.4	11.2
Distance of parietal foramen in front of end skull table, T	4.8	4	3
Breadth of snout 1/5th of skull length from tip, S	17.4	10.8	9.2
Midline orbital length, U	3.8	3.3	2.5
Length of interpterygoid, Y	10.4	7.2	5.7
Breadth of interpterygoid, Z	6	4	3.3
Distance of exoccipital behind skull table	5	2.2	2

parabolic skulls; orbits far forward; postorbital part of skull very long; narrow internarial width; lateral line grooves well defined; extension of supraorbital lateral line canal onto parietal bone.

3. B. watsoni may be defined as a large Batrachosuchus; skull broader than that of B. browni; greater internarial width; greater interorbital breadth; longer preorbital region; shorter orbits; longer postorbital deck; lateral line canals well defined and broad; parasphenoid reaches limit of skull base; depression in centre of vomer; one lateral line canal present on postfrontal.

4. B. browni may be defined as a large Batrachosuchus; skull relatively narrower than that of B. watsoni; narrower interorbital breadth; shorter preorbital region; longer orbits; shorter postorbital deck; lateral line canals well defined, but relatively much narrower and of more U-shaped in section than in B. watsoni; parasphenoid does not reach skull limit; vomerine foramen in centre of vomer; 3 lateral line canals present on postfrontal; evidence of paired tusks on vomer, palatine and ectopterygoid.

5. B. concordi may be defined as a small Batrachosuchus with a skull narrower than B. browni and much narrower than B. watsoni; interorbital breadth very much narrower than both B. browni and B. watsoni; shorter preorbital length than B. browni, much shorter than B. watsoni; orbit slightly smaller than B. browni; postorbital length greater than B. browni, but shorter than B. watsoni; interpterygoid vacuity shorter than B. browni and much shorter than B. watsoni; interpterygoid vacuity narrower than both B. watsoni and B. browni; distance of parietal foramen from posterior of skull table greater than both B. browni and B. watsoni; lateral line canals weakly defined; parasphenoid reaches limit of skull; exoccipital does not project as far posteriorly as in either B. browni or B. watsoni; in addition a lingual process of the angular is present (the jaws of the other two species of Batrachosuchus are unknown).

6. B. concordi is more or less on the same evolutionary level as the Cynognathus zone brachyopids, thus tending to support other evidence that the N'tawere Formation is probably of a similar age, and probably Early Middle Triassic (Chernin and Cosgriff, 1975).

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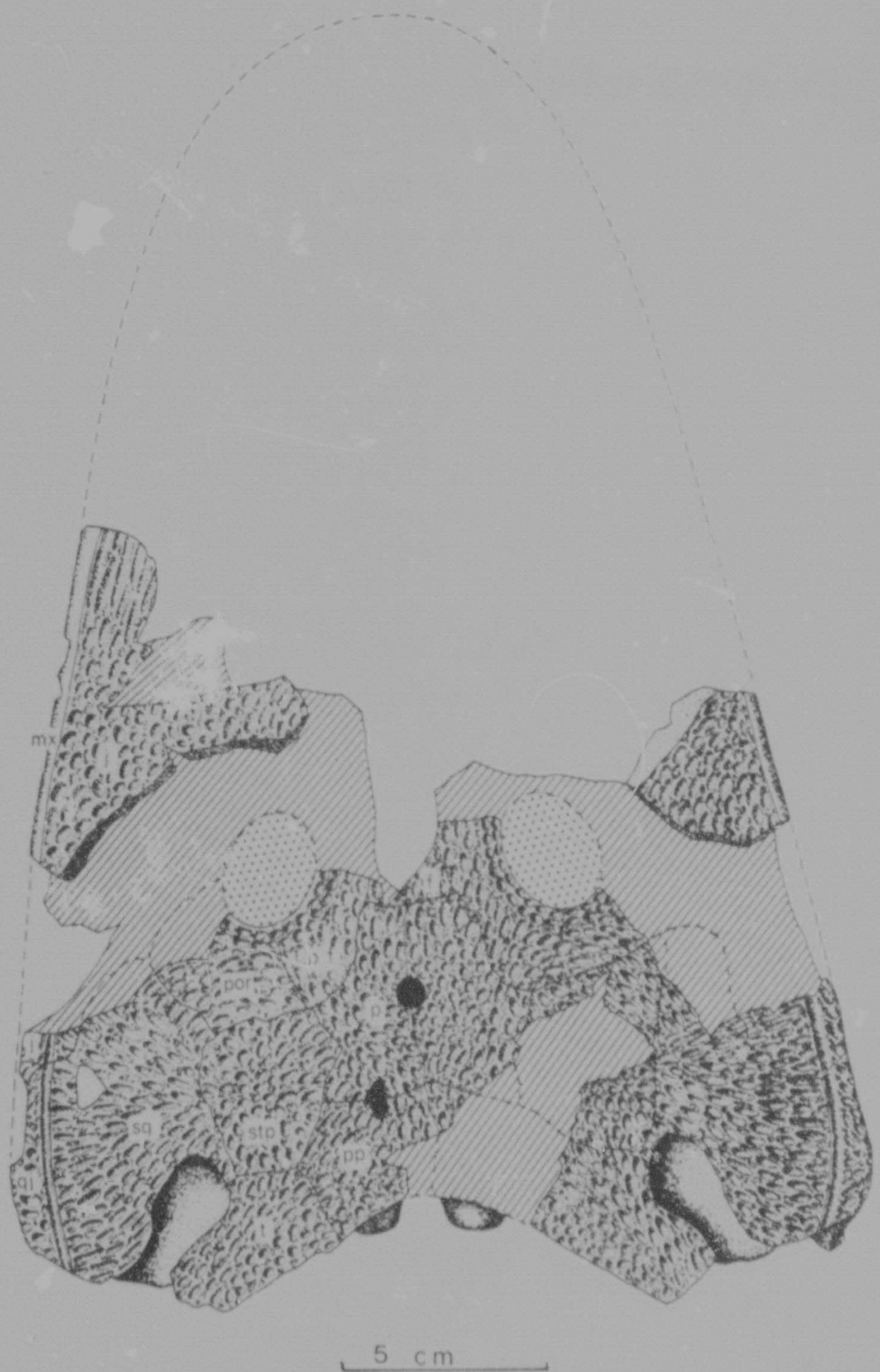

Fig. 1a

Figure 1. (a) Dorsal view of *Parotosaurus africanus*

(b) Palatal view of *Parotosaurus africanus*

(c) Posterior view of *Parotosaurus africanus*

(d) Lateral view of *Parotosaurus africanus*